PROC. ENTOMOL. SOC. WASH.
105(1), 2003, pp. 30–49

A REVISION AND PHYLOGENETIC STUDY OF *LIPOCHAETA* COQUILLETT (DIPTERA: EPHYDRIDAE)

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Abstract.—The genus *Lipochaeta* Coquillett is revised and a phylogenetic analysis of the genera of the tribe Lipochaetini is provided. *Lipochaeta* is known thus far only from the New World, where there are now two species. The second species, ***L. ranica*, n. sp.**, (type locality: California), is described herein. The species of *Lipochaeta* occur in saline or alkaline habitats, especially along maritime coasts. The monophyly of *Lipochaeta* is well corroborated and its putative sister group is the Old World genus *Homalometophus* Becker.

Key Words: revision, Diptera, Ephydridae, Lipochaetini, *L. ranica*, New World, phylogeny

Among 114 genera of shore flies (Diptera: Ephydridae), less than 17% (19 genera) are monotypic (Mathis and Zatwarnicki 1995), and that percentage is decreasing as we better sample the extant fauna and discover additional species. Field work during the last two decades, for example, has revealed hundreds of new species but very few new genera. There is also a decrease in monotypic genera as we clarify and recharacterize higher level taxa to be more inclusive, monophyletic clades, usually comprising more than one species. The genus *Lipochaeta* Coquillett, the subject of this revision, is an example of this evolving pattern in the classification of shore flies.

Coquillett (1896) described *Lipochaeta slossonae* in the late 19th Century, and until now it was the only included species in the genus. Coquillett recognized that this new genus and species were unusual and appropriately suggested that they be placed in a separate and new subfamily, but he did not provide a subfamilial name. Becker (1896: 275) quoted Coquillett's entire paper but substituted "Lipochaetinae" for *Lipochaeta* in the introductory portion, thus making the subfamilial name available. Attribution of Lipochetinae as a family-group name to Becker was followed in all recent catalogs and is continued here. Sabrosky (1999: 179), however, suggested that, "It seems reasonable to correct the obvious lapse and credit Coquillett with the subfamily." Coquillett clearly was the first person to recognize these taxa, from species to subfamily, but the subfamilial name is correctly attributed to Becker and the generic and species names to Coquillett.

The bizarre external appearance of *Lipochaeta*, being highly adapted to psammophilous habitats, initially confused some authors about its familial affiliation. A year after its description, Williston (1897: 8) preferred placement of *Lipochaeta* ". . . among the Ochthiphilinae in the vicinity of *Rhic-*

noessa [Tethinidae]" and added that, "No Ephydrid that I know of lacks bristles, while both of these latter families [Oscinidae and Agromyzidae] have numerous forms without them. The face is too short, the antennae too different in structure to belong with the Ephydridae. Moreover the pollinose body and white wings, while not absent among Ephydridae, are not at all common." Townsend (1898: 168) described a second species in *Lipochaeta* (*L. texensis* from Padre Island, Texas) and commented on the taxonomic placement of the genus. Townsend wrote that while *Lipochaeta* is ". . . clearly allied to the Ephydridae" it ". . . is truly one of singular aspect and anomalous position." Aldrich's (1905) catalog of Nearctic Diptera followed Coquillett and Townsend in listing *Lipochaeta* as a genus in the Ephydridae and also in placing *L. texensis* as a junior synonym of *L. slossonae*. The synonymy of *L. texensis* with *L. slossonae* was apparently based on information in a letter that Williston had written to Aldrich. Although Jones (1906) did not accept *Lipochaeta* as a shore fly in his worldwide catalog of Ephydridae, he offered no alternative placement. Nearly all subsequent authors have followed Coquillett, Townsend, and Becker in recognizing *Lipochaeta* as an ephydrid, usually in the tribe Lipochaetini, subfamily Parydrinae (Sturtevant and Wheeler 1954; Wirth 1965, 1968; Mathis 1977; Cogan 1980). A notable exception was E. T. Cresson, Jr., the doyen of 20th Century shore-fly workers, who was silent on the subject.

Although recognition of *Lipochaeta* as an ephydrid is now virtually universal, its placement in available shore-fly classifications, especially in catalogs, has varied. Cresson's successors (Sturtevant and Wheeler 1954; Wirth 1965, 1968; Mathis 1977; Cogan 1980) accorded tribal status to the genus in the subfamily Parydrinae, apparently considering *Lipochaeta* to be related to the tribes Parydrini and Hyadinini. Giordani Soika (1981), however, was of the opinion that the tribe Lipochaetini is related to *Isgamera* Giordani Soika and *Asmeringa* Becker, two Old-World genera that occur on the seashores of the Mediterranean and East Africa. Giordani Soika further suggested that the occurrence of Lipochaetini in the New World was due to continental drift and that the group has greater antiquity than was previously thought. Mathis (1984a) concurred with Giordani Soika in removing *Lipochaeta* from Parydrinae and in placing it close to *Isgamera* and *Asmeringa* in the subfamily Gymnomyzinae.

The above-cited studies were based on phenetic or overall differences and similarities, and although the placement of *Lipochaeta* did change from Parydrinae to Gymnomyzinae, its position close to *Isgamera* and *Asmeringa* is unsupported. Although the latter two genera appear similar externally, these features represent, for the most part, independent and convergent adaptations to psammophilous environments that are associated with seashores, not synapomorphies that indicate phylogenetic relationships.

Another advance in the phylogenetic position and composition of Lipochaetini was the recognition that the tribe Atissini, as then characterized, was polyphyletic and included genera that are more closely related to *Hecamede* Haliday (tribe Hecamedini, Mathis 1993) and to *Lipochaeta* (tribe Lipochaetini, Zatwarnicki 1992, Mathis 1995a). Zatwarnicki (1992) provided evidence indicating that the tribe Atissini is related to taxa in the subfamily Hydrelliinae, whereas Hecamedini and Lipochaetini are in the subfamily Gymnomyzinae. Zatwarnicki (1992) cited further evidence that Hecamedini and Lipochaetini are sister groups. The principal source of characters (synapomorphies) for these studies derives from structures of the male terminalia. The latter studies, especially Zatwarnicki (1992), indicate that the tribe Lipochaetini is closely related to the tribe Hecamedini and includes the following four genera (date and author(s) who first placed the genus in Lipochaetini are noted in parenthesis): *Glenanthe* (Mathis and Zatwarnicki 1990b), *Paraglenanthe* Wirth (Zatwarnicki 1992), *Lipochaeta* (Becker 1896), and *Homalometopus* Becker (Mathis 1984b). Recent revisionary and phylogenetic studies of genera of the tribe Lipochaetini include *Homalometopus* (Mathis 1984b, Munari 1988) and *Glenanthe* (Mathis 1992).

Methods and Materials

The descriptive terminology, with the exceptions noted in Mathis (1986) and Mathis and Zatwarnicki (1990a), follows that published in the *Manual of Nearctic Diptera* (McAlpine 1981). Because specimens are small, usually less than 3.5 mm in length, study and illustration of the male terminalia required use of a compound microscope. We have followed the terminology for most structures of the male terminalia that other workers in Ephydridae have used (see references in Mathis 1986; Mathis and Zatwarnicki 1990a, b). The terminology for structures of the male terminalia is provided directly on Figs. 17–18. The species descriptions are composite and not based solely on the holotypes. One head and two venational ratios that are used in the descriptions are defined below (all ratios are based on three specimens: the largest, smallest, and one other). Gena-to-eye ratio is the genal height measured at the maximum height divided by the eye height. Costal vein ratio is the straight line distance between the apices of R_{2+3} and R_{4+5} divided by the distance between the apices of R_1 and R_{2+3}. M vein ratio is the straight line distance along vein M between crossveins (dm-cu and r-m) divided by the distance apicad of dm-cu.

The phylogenetic analysis was performed with the assistance of Hennig86©, a computerized algorithm that produces cladograms by parsimony. Character data were polarized primarily using outgroup procedures. Although autapomorphies were not included in the cladistic analysis (they were made inactive), which would skew the consistency and retention indices, we listed them on the cladogram and included them as part of generic treatments and phylogenetic considerations to document the monophyly of the lineages, particularly at the generic level.

Although many specimens for this study are in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), we also borrowed and studied numerous specimens that are deposited in the following museums:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, USA.
AMNH	American Museum of Natural History, New York, USA.
BMNH	The Natural History Museum (formerly the British Museum (Natural History)), London, England, United Kingdom.
CNC	Canadian National Collection, Ottawa, Canada.

Systematics

Tribe Lipochaetini Becker

Lipochaetini Becker 1896: 275 [as Lipochaetinae]. Type genus: *Lipochaeta* Coquillett 1896.—Zatwarnicki 1992: 89, 118–119 [listing of included genera, phylogenetic placement].—Mathis and Zatwarnicki 1995: 160–163 [world catalog].—Mathis 1995a: 2–4 [description, key to genera].

Diagnosis (synapomorphies indicated by an asterisk (*)).—*Head:* Frontal vitta (or ocellar triangle) setulose*; ocellar seta either greatly reduced or absent (sometimes with a pair of intrafrontal setae slightly larger than other setulae, this pair inserted in front of anterior ocellus)*; pseudopostocellar seta reduced or lacking*; fronto-orbital setae 3 (reduced secondarily in *Lipochaeta*), anterior 2 setae proclinate, posterior seta reclinate. Pedicel lacking prominent, spinelike seta; arista with cuticular hair dorsally and ventrally, appearing macropubescent or brushlike, without dorsal rays*. Eye bearing numerous interfacetal microsetulae (apparently arising from each interfacet). Genal seta reduced or lacking.

Thorax: Dorsocentral setae weakly developed, only posteriormost pair conspicuous; acrostichal setulae in 2–4 rows, frequently with a prescutellar pair better developed; postsutural supra-alar seta lacking; frequently postpronotal and presutural supra-alar seta reduced or lacking; posterior notopleural seta inserted above level of anterior seta, sometimes only slightly so (as in *Homalometopus* and *Lipochaeta*). Wing with vein R_{2+3} long, extended nearly to level of apex of vein R_{4+5}. Legs lacking conspicuous setae; femora and tibiae usually gray to pale brown; tarsi yellow.

Abdomen: 5th tergite of male longer than 4th. Male terminalia as follows: epandrium attenuate, either emarginate posteriorly or incomplete dorsally; surstylus well developed, usually elongate, frequently as long or longer than epandrium; aedeagus elongate, slender, tubular, apex with recurved flap oriented posterodorsally, apical flap in groove at rest, base of aedeagus bifurcate, sometimes with arms elongate*; ejaculatory apodeme present, compressed laterally*; aedeagal apodeme L-shaped, sometimes with extended ventromedial process; gonites (pre- and postgonites) lacking, possibly fused with hypandrium*; hypandrium well sclerotized, usually V- or U-shaped; 5th sternite deeply V- or U-shaped into which the surstyli and aedeagus lie at rest.

Natural history.—This tribe is unusually tolerant of alkaline or saline aquatic environments, and species of most genera occur on seashores or are associated with inland aquatic habitats that are saline or alkaline.

Discussion.—Although the tribe Lipochaetini and each of the included genera are readily characterized, often with substantial evidence that they are monophyletic, the relationships among the genera are not well understood. In the key that follows, for example, we have included numerous characters, nearly all autapomorphies, that facilitate identification of the genera but contribute virtually nothing to resolution of their phylogenetic relationships. A further complicating factor is the debatable status or polarity of the few characters that may indicate relationships. For example, a gaping oral cavity and a wide clypeus are character states that are common to *Lipochaeta* and *Homalometopus*, whereas a narrow oral opening and clypeus occur in *Glenanthe* and *Paraglenanthe*. The problem is that both the narrow and wide conditions occur in the outgroup, Hecamedini, as well as commonly elsewhere in the Ephydridae, thus confusing issues about which character state is apomorphic within the Lipochaetini.

The tribe Lipochaetini, which is one of six tribes now placed in the subfamily Gymnomyzinae (Mathis and Zatwarnicki 1995), appears to be most closely related to the tribe Hecamedini (Zatwarnicki 1992). Lipochaetini's sister-group relationship with Hecamedini is corroborated by two synapomorphies that we have identified (including Zatwarnicki's [1992] characters 59–60): 1) pre- and postgonites apparently fused or greatly reduced; 2) posterior notopleural seta inserted much farther dorsad from notopleural suture than anterior seta.

Lipochaetini are distinguished from Hecamedini and other tribes of the subfamily Gymnomyzinae and the tribe's monophyly is confirmed by the following characters (synapomorphies are noted by an asterisk (*)): 1) body densely invested with microtomentum, generally dull colored; *2) ocellar seta lacking or weakly developed; *3) pseudopostocellar seta lacking; *4) arista microsetulose, lacking dorsal rays; *5) frontal vitta bearing many setulae; 6) posterior margin of gena broadly rounded onto occiput; 7) scutellum with 2 pairs of marginal setae; 8) foreleg normal, forefemur slender, foretibia not having a large spur apically; 9) abdominal tergites 2–4 subequal in width, microtomentose, but more or less smooth; *10) aedeagus with apical flap or appendix that is folded back dorsally; and *11) gonite reduced.

With the phylogenetic background of the tribe Lipochaetini within the subfamily Gymnomyzinae established and the monophyly of Lipochaetini documented, we now

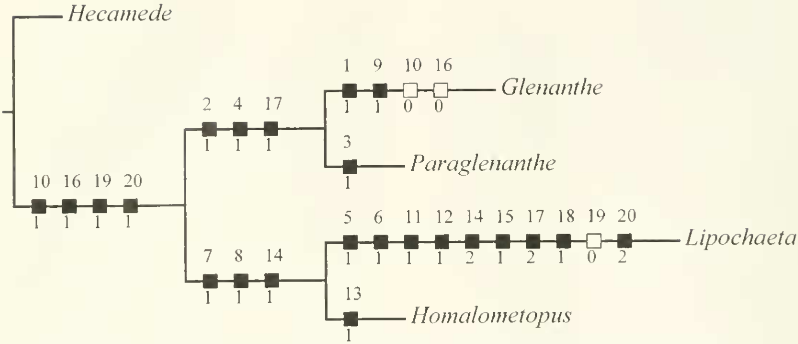


Fig. 1. Cladogram depicting hypothetical cladistic relationships among genera of Lipochaetini (length 17 steps, consistency index 0.82; retention index 0.62).

proceed with the cladistic analysis and resultant relationships among the included genera, but with a few explanatory remarks first. In the presentation on genus-level relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed by a discussion to explain its states and to provide perspective and any qualifying comments about that character. After presentation of the information on character evidence, a hypothesis of the cladistic relationships is presented and briefly discussed. The cladogram (Fig. 1) is the primary mode to convey relationships, and the discussion is to supplement the cladogram and is intended only to complement the latter. In the discussion of character data, a "0" indicates the state of the outgroup; a "1" or "2" indicates the derived states. All multistate characters (7, 14, 17, and 20) were treated as nonadditive (−), and characters 1, 3, 5, 6, 9, 11, 12, 15, and 18, which are autapomorphies for various genera or tribes, were made inactive (]) for the analysis so that they do not alter the calculation of the consistency index. The numbers used for characters in the presentation are the same as those on the cladogram, and the sequence is the same as noted in the character matrix (Table 1). The genus *Hecamede*, which is the nominate genus for the tribe Hecamedini, was the outgroup in our phylogenetic analysis.

Table 1. Matrix of characters and taxa used in the cladistic analysis of Lipochaetini (numbers for characters correspond with those used in the text).

Taxa	Characters 000000000 123456789	 1111111 0123456	 1112 7890
Hecamede	000000000	0000000	0000
Glenanthe	110100001	0000000	1011
Lipochaeta	000011110	1110211	2102
Homalometopus	000000110	1001101	0011
Paraglenanthe	011100000	1000001	1011

Characters Used in the Phylogenetic Analysis

(Running Count in Parenthesis.)

Head

1(1). Shape of eye: (0) round or oval; (1) pyriform (an autapomorphy for *Glenanthe*).

2(2). Shape of clypeus: (0) wide, bandlike; (1) narrow (a synapomorphy for *Glenanthe* and *Paraglenanthe*).

3(3). Shape or ventral facial margin: (0) flat; (1) emarginate (an autapomorphy for *Paraglenanthe*).

4(4). Oral opening: (0) wide, gaping; (1) narrow (a synapomorphy for *Glenanthe* and *Paraglenanthe*).

5(5). Height of face: (0) normal, usually higher than wide; (1) short (an autapomorphy for *Lipochaeta*).

6(6). Size of antenna: (0) normal; (1) reduced, especially the arista (an autapomorphy for *Lipochaeta*).

7(7). Distance between antennal bases: (0) narrow, distance between antennal bases less than antennal width; (1) wide, antennal bases separated by width greater than antennal width (an autapomorphy for *Homalometopus*); (2) very wide, antennal bases separated by 3× antennal width (an autapomorphy for *Lipochaeta*).

8(9). Shape of mesofrons: (0) narrow, V-shaped, with wide parafrons and fronto-orbits (*Glenanthe* and *Paraglenanthe*); (1) wide, broadly U-shaped, parafrons and fronto-orbits comparatively smaller (a synapomorphy for *Homalometopus* and *Lipochaeta*).

9(9). Height of gena: (0) high, 0.33 to more than 0.5× eye height; (1) short, less than ⅛ eye height (an autapomorphy for *Glenanthe*).

Thorax

1(10). Katepisternal seta: (0) present, conspicuous, well developed; (1) greatly reduced (a synapomorphy for *Homalometopus*, *Lipochaeta*, and *Paraglenanthe*).

2(11). Postpronotal seta: (0) present; (1) reduced (an autapomorphy for *Lipochaeta*).

3(12). Presutural supra-alar seta: (0) present; (1) absent (an autapomorphy for *Lipochaeta*).

4(13). Position of posterior notopleural seta: (0) inserted above level of anterior seta; (1) inserted at about same level as anterior seta or only slightly elevated (a synapomorphy for *Homalometopus* and *Lipochaeta*).

5(14). Setae along posterior margin of anepisternum: (0) 2 setae and some smaller setulae; (1) 1 seta (an autapomorphy for *Homalometomus*); (2) no large setae, only setulae (an autoapomorphy for *Lipochaeta*).

6(15). Wing near apex of subcostal vein and vein R_1: (0) normal, membranous; (1) sclerotized and thickened, yellow (an autapomorphy for *Lipochaeta*).

7(16). Wing membrane coloration: (0) hyaline, transparent; (1) white, translucent (a synapomorphy for *Glenanthe*, *Paraglenanthe*, and *Lipochaeta*).

Abdomen

1(17). Epandrium: (0) entire dorsally; (1) attenuate with a posterodorsal notch (an autapomorphy for *Glenanthe* and *Paraglenanthe*); (2) incomplete dorsally with a gap between two lateral portions (an autapomorphy for *Lipochaeta*).

2(18). Cerci: (0) separate, unfused with medial margin of epandrium; (1) fused laterally with median margin of epandrium (an autapomorphy for *Lipochaeta*).

3(19). Length of surstylus: (0) about same length as epandrial length; (1) much longer than epandrial length, usually by more than twice (a synapomorphy for *Homalometopus*, *Glenanthe*, and *Paraglenanthe*).

4(20). Base of aedeagus: (0) truncate or nearly so; (1) bifurcate (a synapomorphy for *Homalometopus* and *Paraglenanthe*); (2) arms of basal bifurcation more elongate and curled beneath (an autapomorphy for *Lipochaeta*).

Analysis and Results

Using the implicit enumeration (ie*) option of Hennig86, which is an exhaustive

Table 2. Analysis of characters based on the cladogram (Fig. 1). Con. Index = Consistency Index; Ret. Index = Retention Index.

	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Steps	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	2	2	1	2	2
Con. Index	100	100	100	100	100	100	100	100	100	50	100	100	100	100	100	50	100	100	50	100
Ret. Index	100	100	100	100	100	100	100	100	100	0	100	100	100	100	100	0	100	100	0	100

search, a single most parsimonious tree was generated from the analysis of the 20 characters. The cladogram has a length of 17 steps and consistency and retention indices of 0.82 and 0.62 respectively. The matrix was then subjected iteratively to successive weighing (xs w, ie*, cc) to determine a character's contribution or weight and to find cladograms supported by the most consistent characters (Carpenter 1988, Dietrich and McKamey 1995). The analysis of the characters for this cladogram is given in Table 2 and the weights of the various characters is given in Table 3. Given these character weights, the analysis of the resultant cladogram resulted in consistency and retention indices of 1.00 and 1.00 respectively.

As indicated on the cladogram (Fig. 1), the tribe Lipochaetini is divided into two basal sublineages. The first basal sublineage comprises half of the genera (number of species in parenthesis): *Lipochaeta* (2) and *Homalometopus* (7), with 9 species. The monophyly of this sublineage is corroborated by characters 7, 8, and 14. From a biogeographic standpoint, this sister-group relationship suggests that the cladogenetic event(s) that resulted in the divergence of *Lipochaeta* and *Homalometopus* occurred some time ago. *Homalometopus* is only found in the Old World where it now has relatively high diversity, i.e., seven species representing several speciation events, especially in the area of the Mediterranean Sea. *Lipochaeta* occurs only in the New World where speciation has been slower, resulting in only two described species and the possibility of a third in Chile.

The second basal sublineage includes the other two genera of Lipochaetini, *Glenanthe* (15) and *Paraglenanthe* (3), with 18 species. The monophyly of this sublineage is corroborated by characters 2, 4, and 17. *Glenanthe* occurs in both the New and Old Worlds, but there is apparently greater species diversity in the New World, assuming the present number of described species is

Table 3. Weights (varying between 1–10) and status (additive = +, nonadditive = −, active = [, inactive =]) of characters after successive weighting.

	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Weight, status	10+]	10+[	10+]	10+[	10+]	10+]	10−[	10+[	10+]	0+[	10+]	10+]	10+]	10−[	10+]	0+[	10−[	10+]	0+[	10−[

a good indicator. *Paraglenanthe*, on the other hand, has a more limited distribution, occurring only in the New World where it is primarily circumcaribbean.

KEY TO GENERA OF LIPOCHAETINI BECKER

1. Eye pyriform, distinctly narrowed ventrally; gena short, less than one-fourth eye height; katepisternal seta present along posterior margin, moderately well developed . . *Glenanthe* Haliday
[15 species, worldwide; Mathis 1995a]
– Eye generally oval or round, not distinctly narrowed ventrally; gena high, one-third or more of eye height; katepisternal seta reduced 2
2. Antenna reduced, inserted in well-separated cavity, arista atrophied, budlike; face short, height subequal to length of reduced antenna; clypeus bandlike; oral opening gaping; body setae and setulae pale; costa distinctly thickened at merger of vein R_1 . . . . . *Lipochaeta* Coquillett
[2 species, New World; mostly costal marine on sand but also inland where saline conditions exist]
– Antenna normally developed, not in deep cavity, arista as long as flagellomere 1; face well developed, height much more than length of antenna; clypeus variable; oral opening narrow or gaping; setae and setulae largely black; costa only slightly thickened at merger of vein R_1 . . 3
3. Mesofrons large, occupying most of frons, platelike, subrectangular, uniformly and evenly setulose; ventral facial margin flat; clypeus wide, bandlike; oral opening large, gaping . . . . *Homalometopus* Becker
[7 species, Eastern Hemisphere (Mediterranean); Mathis 1984b, Munari 1988]
– Frons lacking differentiated mesofrons, at most with frontal or ocellar triangle or vitta that is weakly differentiated from remainder of frons; ventral facial margin emarginate; clypeus narrow, exposed through ventral facial emargination; oral opening small . . *Paraglenanthe* Wirth
[3 species, New World (Caribbean); Wirth 1956]

Genus *Lipochaeta* Coquillett

Lipochaeta Coquillett 1896: 220. Type species: *Lipochaeta slossonae* Coquillett 1896, original designation.—Becker 1896: 274–275 [quote of original description].—Williston 1897: 7 [placement near *Rhicnoessa*, family Agromyzidae, subfamily "Ochthiphilinae"]; 1908: 306 [generic key].—Townsend 1898: 168 [notes on generic placement].—Aldrich 1905: 631 [Nearctic catalog].—Jones 1906: 169 [note, diagnosis].—Curran 1934: 346–347 [figs. of head, generic key].—Sturtevant and Wheeler 1954: 215–216 [listed as a genus in Napeae].—Wirth 1965: 750 [Nearctic catalog]; 1968: 22 [Neotropical catalog].—Mathis and Zatwarnicki 1995: 163 [world catalog].

Diagnosis.—*Lipochaeta* is distinguished from other genera of Lipochaetini by the following combination of characters: Body setae and setulae generally inconspicuous, pale. Antennae widely separate and arista rudimentary. Frons projected and large; sub-cranial cavity large, gaping. Body length 2.0–4.0 mm, generally grayish, dorsum of head and thorax sometimes brownish, and almost entirely microtomentose.

Description.—*Head:* Wider than high in anterior view, grayish; entirely microtomentose, sparsely setulose; mesofrons wide, broadly U-shaped, uniformly setulose, differentiated from remainder of frons by darker gray to brownish gray; parafrons a comparatively small triangular anterior area; fronto-orbits comparatively narrow. Head without conspicuous setae. Ocellar setae absent; pseudopostocellar setae absent, fronto-orbital setae absent (reduced secondarily); ocelli arranged to form equilateral triangle. Antenna reduced, in well-separated (gap between antennal bases about 3× antennal width), deep cavities, oriented laterally; pedicel with fine, pale setulae on ventral and dorsal sides, but lacking dorsoapical seta, arista rudimentary and budlike. Eye generally irregularly round with distinct, angular margin posterodorsally near vertex; interfacetal microsetulae present, numerous, conspicuous. Face short, height subequal to length of reduced antenna, narrowly triangular in profile, tapered to acute angle posteroventrally; clypeus bandlike, wide. Gena bearing fine, pale setulae. Subcranial cavity large and gaping.

Thorax: Entirely grayish to brownish, microtomentose, pleural area generally paler than dorsal coloration; mesonotum bearing numerous, fine, pale setulae, setulae most conspicuous on posterior portion of scutellum, particularly in females; postpronotal seta reduced; posterior notopleural seta at only slightly elevated position relative to anterior seta; anepisternum bearing numerous setulae; katepisternal seta variable. Wing with costal vein extended to vein M; costa distinctly thickened at merger of vein R_1; dorsal setulae along costal vein ended just beyond vein R_{2+3}; wing white, translucent, wing venation and halter yellow. Midfemur bearing comblike row of 6–7 white, longer setae anteriorly at apical ⅓–½; tarsi yellowish; midtarsus with basitarsomere longer than remaining four; each tarsomere with dark, ventroapical setae; midtarsus bearing twice as many black setae as others, these paired at apices of tarsomeres, basitarsomere bearing 4–5 pairs, apical tarsomere variable; pulvillus present.

Abdomen: Male: tergites 2–4 about equal in length; length of 5th tergite slightly more than combined length of 3rd and 4th tergites; 5th tergite triangular in dorsal view; sternites 2–4 linear, much narrower than long, weakly sclerotized; 5th sternite deeply U-shaped and better sclerotized along inner margin of U. Male Terminalia: epandrium greatly reduced, in lateral view about as long as cerci, fused dorsolaterally with cerci, incomplete dorsally, with a gap between lateral portions; surstylus digitiform, moderately to conspicuously elongate, mostly parallel-sided, usually shallowly curved in lateral view, generally evenly setulose, setulae longer apically; gonites either indistinguishably fused with hypandrium or lacking; ejaculatory apodeme evident as a simple, slightly angulate, long, narrow process; aedeagus very long, narrow, tubular, length twice or slightly longer than surstylus, apex with membranous flap folded back on itself, length of flap about ¼–⅓ length of aedeagus, basal portion of aedeagus angled ventrally and forked with aedeagal apodeme between arms of basal fork; hypandrium well sclerotized, more or less Y-shaped in ventral view, with forked portion basal, lateral phalanges from basal arms of fork. Female Terminalia: Segments 6–7 telescoped out to form tube; 8th segment apparently lacking; hypoproct Y-shaped.

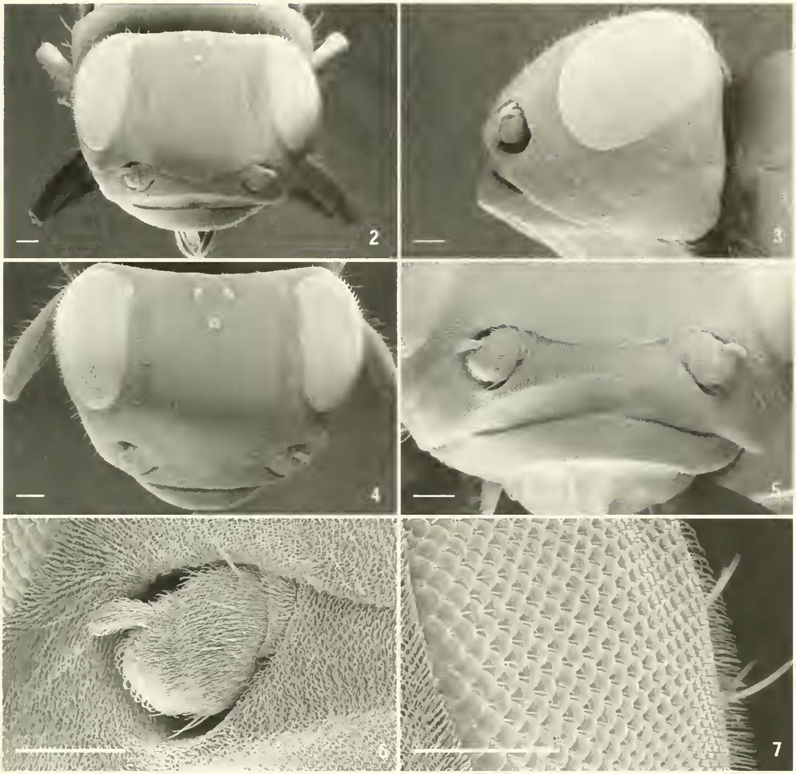
Remarks.—The poorly developed epandrium and an aedeagus with a terminal membranous flap are similar to *Glenanthe* and *Homalometopus* Becker. The female terminalia is also similar to that of *Homalometopus.*

Until now, *Lipochaeta* has been monotypic, with *L. slossonae* as the only included species. The second species, *L. ranica,* is very similar and obviously closely related. Differences between these two species are seemingly slight but are consistent and significant (see key and descriptions of species below). In addition to describing a second species, which is found primarily on the west coast of California and Mexico, we also report the possibility of a third species from Chile. The potential third species is represented by two female specimens from Atacama. One of the females has an elongate scutellum and bears a fringe of long, white setulae along the margin. An elongate scutellum also occurs in *L. slossonae* and *L. ranica,* and to a degree, the scutellar fringe of setulae is also apparent within the variation of these two species. Thus we are unsure about the status of the Chilean specimens, i.e., is the variation in the scutellar features intra- or interspecific. Additional specimens, especially males, are needed to assess better these possibilities.

KEY TO SPECIES OF *LIPOCHAETA*

1. Tarsi often entirely yellow; surstylus elongate (distinctly longer than height of epandrium), tapered apically to narrowly rounded apex (east coast of North America from Massachusetts south to Florida and Texas, islands of the Caribbean, Belize [Stann Creek], Mexico [Chiapas], and Panama [Playa Santa Clara] . . . . *L. slossonae* Coquillett

– Apical tarsomere always slightly to distinctly darkened; surstylus shorter (subequal to height of epandrium), parallel sided to bluntly rounded apex (west coast of North America from



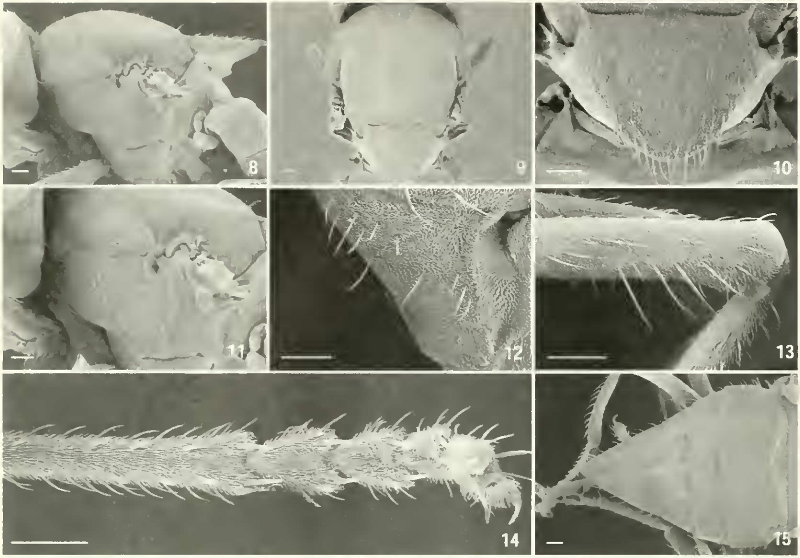
Figs. 2–7. Scanning electron micrographs of *Lipochaeta slossonae*. 2, Head, anterodorsal view. 3, Same, lateral view. 4, Frons, anterodorsal view. 5, Face, anterior view. 6, Right antenna, anterior view. 7, Left compound eye and interfacetal setae, anterior view. Scale bars equals 100 μm.

San Francisco south to the Mexican states of Baja California Sur and Nayarit, and to the Galápagos Islands) . . . . *L. ranica*, new species

Lipochaeta slossonae Coquillett
(Figs. 2–19)

Lipochaeta slossonae Coquillett 1896: 220.—Becker 1896: 275 [description].—Aldrich 1905: 631 [Nearctic catalog (partim)].—Jones 1906: 169 [note, diagnosis].—Johnson 1913: 86 [list, Florida].—Sturtevant and Wheeler 1954: 216 [list, Florida, Maryland, New Jersey, Texas, comments on habitat and behavior].—Wirth 1956: 18 [list, Bahamas]; 1965: 751 [Nearctic catalog (partim)]; 1968: 22 [Neotropical catalog (partim)].—Foote 1995: 422 [sandy beach habitat].—Mathis and Zatwarnicki 1995: 163 [world catalog (partim)].—Mathis 1997: 28–29 [review, Belize].

Lipochaeta texensis Townsend 1898: 168.—Aldrich 1905: 631 [synonymy].—



Figs. 8–15. Scanning electron micrographs of *Lipochaeta slossonae*. 8, Thorax, lateral view. 9, Same, dorsal view. 10, Scutellum, dorsal view. 11, Pleural area, lateral view. 12, Anepisternum, dorsoblique view. 13, Left midfemur, anterior view. 14, Left midtarsus, ventral view. 15, Abdomen, dorsal view. Scale bar equals 100 µm.

Sturtevant and Wheeler 1954: 216 [synonymy]. Diagnosis.—Moderately small to moderately large shore flies, body length 2.0–4.0 mm.

Description.—*Head* (Figs. 2–7): In profile as long as high. Mesofrons slightly differentiated by darker brown or gray microtomentum. Setae and setulae generally inconspicuous; genal setulae shorter than anepisternal setulae.

Thorax (Figs. 8–16): Mesonotum varying from slightly darker brown to gray. Anepisternal setae moderately long; katepisternal seta reduced. Wing as in Fig. 16. Tarsi usually yellow, apical tarsomere slightly darkened in some specimens.

Abdomen (Figs. 17–18): Surstylus elongate (distinctly longer than height of epandrium), tapered apically to narrowly rounded apex.

Type material.—Described from two ♂. The lectotype ♂ of *Lipochaeta slossonae* Coquillett, here designated to preserve stability and make more universal the use of this name, is labeled "CH[arlotte]. H[ar]B[o]R. FL[orid]A [folded]/Mrs-Slosson Collector/Type No 4300 U.S.N.M. [red; "4300" handwritten]/Lipochaeta slossonae Coq. [handwritten; black sub-border." The lectotype is double mounted (glued to a paper triangle along with a second specimen, also a male, that lacks its head), is in good condition, and is deposited in the USNM (4300). Coquillett (1896) wrote that the two syntypes were specifically from Punta Gorda, which is a city on the eastern shore of Charlotte Harbor bay. The second male is a paralectotype.

The syntype(s) of *Lipochaeta texensis* is from USA. Texas: Cameron County, Padre Island; ST (sex ?), BMNH. We were unable to locate this specimen, which apparently was in the BMNH. Its whereabouts is unknown.

Other specimens examined.—ANGUILLA. Long Pond Bay (18°13′N, 63°01′W), 29 Mar 1992, W. E. Steiner, J. M. Swearingen (37 ♂, 41 ♀; USNM); Prickly Pear, (18°16′10″N, 63°10′30″W), 30 Mar 1992, W. E. Steiner, J. M. Swearingen (7 ♂, 11 ♀; USNM); Sandy Ground (18°12′20″N, 63°05′30″W), 24–30 Mar 1992, W. E. Steiner, J. M. Swearingen (2 ♀; USNM).

BAHAMAS. *Great Inagua Island:* Matthew Town, 31 Jan 1953, E. B. Hayden, G. B. Rabb (1 ♀; AMNH). *Turks and Caicos Islands:* Grand Turk Island, 19 Feb 1953, E. B. Hayden (3 ♂, 2 ♀; AMNH); South Caicos Island, 11 Feb 1953, E. B. Hayden (1 ♂, 3 ♀; AMNH).

BELIZE. *Stann Creek:* Carrie Bow Cay, 31 May 1985, W. N. Mathis (2 ♂, 4 ♀; USNM).

CUBA. *Sancti Spiritus:* La Boca (4 km S; 21°45.9′N, 80°01.5′W), 12 Dec 1994, W. N. Mathis (8 ♂, 3 ♀; USNM); Playa Ancón (21°44.1′N, 79°59.9′W), 12 Dec 1994, W. N. Mathis (2 ♂, 3 ♀; USNM).

CURAÇÃO. Coral Specht (3 km E Willemstad), 8–15 Feb 1987, W. E. Steiner, J. M. Swearingen (1 ♀; USNM).

DOMINICAN REPUBLIC. *Azua:* Puerto Viejo (18°20.9′N, 70°50.4′W), 14 May 1995, W. N. Mathis (2 ♂, 2 ♀; USNM). *Barahona:* Barahona (18°12′N, 71°5.3′W), 20 May 1998, D. and W. N. Mathis (4 ♂, 1 ♀; USNM). *La Romana:* Isla Saona, Mano Juan (18°08.1′N, 68°44.5′W), 13 May 1995, W. N. Mathis (11 ♂, 2 ♀; USNM). *Monte Cristi:* Monte Cristi (beach; 19°51.5′N, 71°39.5′W), 18 May 1995, W. N. Mathis (6 ♂; USNM).

GRAND CAYMAN. Double Head (19°23.4′N, 81°22.3′W), 27 Apr 1994, D. and W. N. Mathis (8 ♂, 4 ♀; USNM).

GUYANA. Mahaica (6°42.8′N, 57°55.6′W), 14 Apr-20 Aug 1994, 1997, W. N. Mathis (1 ♂, 1 ♀; USNM).

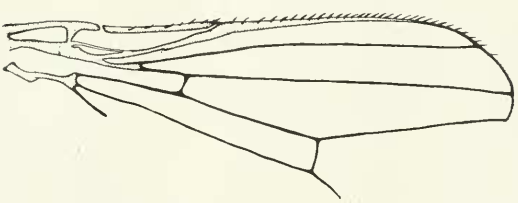
JAMAICA. *Clarendon:* Barnswell Beach (17°45′N, 77°08.5′W), 13 May 1996, D. and W. N. Mathis, H. Williams (1 ♂; USNM); Farquhars Beach (17°50.9′N, 77°22.8′W), 9 May 1996, D. and W. N. Mathis, H. Williams (5 ♂, 5 ♀; USNM); Jackson Bay (17°44.7′N, 77°12.6′W), 13 May 1996, D. and W. N. Mathis, H. Williams (6 ♂, 3 ♀; USNM). *St. Elizabeth:* Great Pedro Pond (17°52.5′N, 77°45.2′W), 19 Apr 2000, W. N. Mathis (4 ♂, 4 ♀; USNM); Salt Pond, Parottee Beach (17°58.1′N, 77°50.2′W), 19 Apr 2000, W. N. Mathis (2 ♀; USNM).

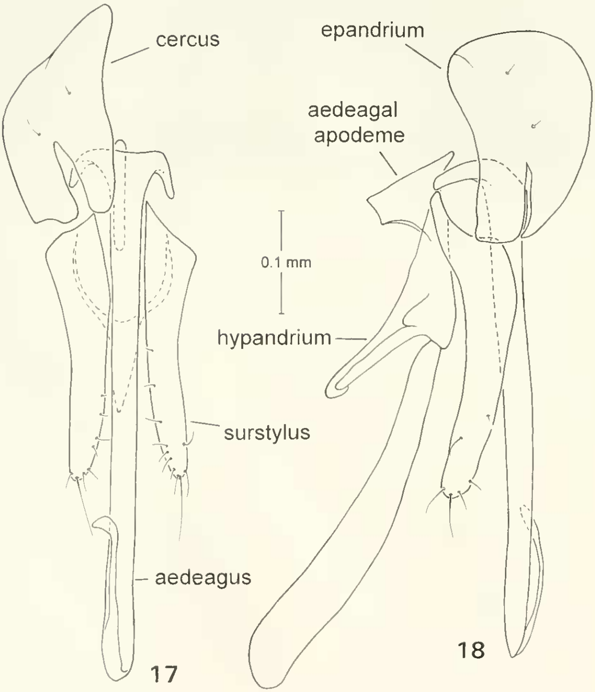
MEXICO. *Chiapas:* Puerto Arista (2 km E), 18 May 1985, A. Freidberg, W. N. Mathis (10 ♂, 31 ♀; USNM).

PANAMA. *Cocle:* Playa Santa Clara, 2 Jul 1967, W. W. Wirth (1 ♂, 1 ♀; USNM).

PUERTO RICO. Bahía Salinas (beach; 17°57.5′N, 67°12′W), 20 Sep 1995, D. and W. N. Mathis (4 ♂, 7 ♀; USNM). Punta Jacinto (near Guanica; 17°57′N, 66°52.6′W), 20 Sep 1995, D. and W. N. Mathis (1 ♂; USNM).

UNITED STATES. *Florida. Charlotte:* Charlotte Harbor (2 ♂; USNM); Punta Gorda, 27 Jan 1932, A. L. Melander (1 ♂; ANSP). *Duval:* Little Talbot Island State Park, 28 May 1953, M. R. Wheeler (2 ♂, 2 ♀; USNM). *Lee:* Bonita Beach, 17 Apr 1970, W. W. Wirth (10 ♂, 19 ♀; USNM); Sanibel Island, Lighthouse Park, 17 Apr 1989, D. and W. N. Mathis (4 ♂; USNM). *Manatee:* Anna Maria, 19 May 1953, M. R. Wheeler (2 ♂, 1 ♀; USNM). *Monroe:* Everglades National Park (on white sand beach), 3 Apr 1958, H. V. Weems, Jr. (1 ♂; USNM); Key West, 5 Feb 1938, A. L. Melander (6 ♂, 4 ♀; ANSP); Matecumbe, 2 Feb 1938, A. L. Melander (2 ♂; ANSP). *Pinellas:* St. Petersburg, 29 Jan-30 Mar 1932, E. T. Cresson, Jr., A. L. Melander (4 ♂, 13 ♀; ANSP). *Georgia. Liberty:* St. Catherines Island, 21 Apr–30 Oct 1977, 1978, A. Hook, R. W. Matthews, J. Krispyn (1 ♂, 1 ♀; USNM). *Chatham:* Chatham (at light), 1 Oct 1953, H. F. Schoof (1 ♂; USNM). *Maryland. Calvert:* Chesapeake Beach, 20 Aug–20 Sep 1914, J. M. Aldrich, N. Banks, G. H. Greene (28 ♂, 15 ♀; ANSP, USNM). *Massachusetts. Barnstable:*





Figs. 16–18. Wing and structures of the male terminalia of *Lipochaeta slossonae* (ejaculatory apodeme not illustrated; Florida. Lee: Bonita Beach). 16, Wing, dorsal view. 17, Cerci (left side only), epandrium (left side only), surstylus, aedeagus, aedeagal apodeme, and hypandrium, lateral view. 18, Same (hypandrium lacking), posterior view. Scale bar equals 0.2 mm.

Sagamore Beach, 14 Jul 1932 (1 ♀; USNM). *Mississippi. Harrison:* Ship Island (north side; 30°12.6′N, 88°58′W), 27 Jun 1962, D. L. Deonier (1 ♀; USNM). *Jackson:* Horn Island (taken in inter-tidal zone on sand surface; 30°15′N, 88°42′W), 13 Jun 1962, D. L. Deonier (1 ♀; USNM). *New Jersey. Cape May:* Cape May, 6 Jun 1971 (1 ♂; ANSP); Wildwood, 18 Jul–18 Sep 1908, 1920, E. T. Cresson, Jr. (25 ♂, 29 ♀; ANSP). *New York. Weschester:* Oak Island, 31 Jul 1913 (3 ♂, 1 ♀; ANSP). *North Carolina. Onslow:* Ashe Island (emergence trap), 7 Oct 1976, T. D. Edwards (2 ♂; USNM). *Oklahoma. Alfalfa:* Cherokee Salt Plains, 18 Jun 1930, R. D. Bird (3 ♂; USNM); Great Salt Plains (salt marsh), 22 May 1969, W. W. Wirth (6 ♂, 3 ♀; USNM). *South Carolina. Beaufort:* Hilton Head Island (UV light trap), 29 May 1980, P. H. Adler (2 ♂; USNM). *Texas. Brazoria:* Freeport, 9 Mar 1951 (1 ♂; USNM). *Calhoun:* Indianola, 28 Apr–5 Jun 1951, 1953 (4 ♂, 1 ♀; USNM). *Cameron:* Port Isabel, 23 Mar–11 Dec 1910, 1951 (1 ♂, 6 ♀; ANSP, USNM). *Galveston:* Galveston, May–26 Dec 1900, 1917, 1951, J. M. Aldrich, F. H. Snow, M. R. Wheeler (21 ♂, 19 ♀; ANSP, USNM). *Kleberg:* Riviera, 23 Mar 1951 (8 ♂, 4 ♀; USNM). *Nueces:* Corpus Christi, 18 Mar 1908, Jones and Pratt (1 ♂, 3 ♀; USNM). *San Patricio:* Sinton, 23 Mar 1951 (2 ♀; USNM).

Distribution (Fig. 19).—Nearctic: USA (FL, GA, MA, MS, NC, NJ, NY, OK, SC, TX). Neotropical: Bahamas, Belize, Curaçao, Guyana, Mexico (CHI), Panama, West Indies (Anguilla, Cuba, Dominican Republic, Grand Cayman, Jamaica, Puerto Rico).

Natural history.—This species occurs on the bare surface of wet, sandy, maritime beaches, especially in embayments and areas where the beach is somewhat protected from the direct and abrading actions of waves. Although saline habitats are primarily coastal maritime, this species also occurs inland, such as in Oklahoma, where beaches associated with saline environments, usually as saline playas, are also found.

Remarks.—Although we were unable to locate and study the syntypes of the junior synonym, *L. texensis*, we are reasonably confident that the specimens are conspecific with the senior synonym and that the synonymy Aldrich (1905) proposed is correct. All specimens we have examined from Texas, including specimens from coastal sites near Padre Island, the type locality of *L. texensis*, are conspecific. If the syntype is found, the question of conspecificity should be confirmed and a lectotype designated.

***Lipochaeta ranica* Mathis and Trautwein, new species**

(Figs. 20–31)

Lipochaeta slossonae of authors, not Coquillett [misidentification].—Townsend 1898: 168 [abundance on seashore in southern California].—Aldrich 1905: 631 [Nearctic catalog (partim), note on abundance in southern California].—Cole 1912a: 838 [note]; 1912b: 161–162 [list, habitus fig.]; 1923: 478 [list, Loreto, Isla Partida]; 1969: 392, 404 [generic key, discussion].—Wirth and Stone 1956: 465, 470 [generic key, list, California].—Wirth 1965: 751 [Nearctic catalog (partim)]; 1968: 22 [Neotropical catalog (partim)].—Cheng and Lewin 1974: 167–168 [behavior, feeding habits].—Mathis 1995b: 4 [Galápagos Islands].—Zatwarnicki 1992: 112 [figs. of male terminalia].—Mathis and Zatwarnicki 1995: 163 [world catalog (partim)].

Diagnosis.—Moderately small to medium-sized shore flies, body length 2.10–3.80 mm.

Description.—*Head* (Figs. 20–23): In profile appearing projected, longer than high. Mesofrons differentiated as dark brown or dark gray. Setae and setulae generally more conspicuous than *L. slossonae*; length of genal setulae equivalent to length of anepisternal setulae, giving a more setulose appearance.

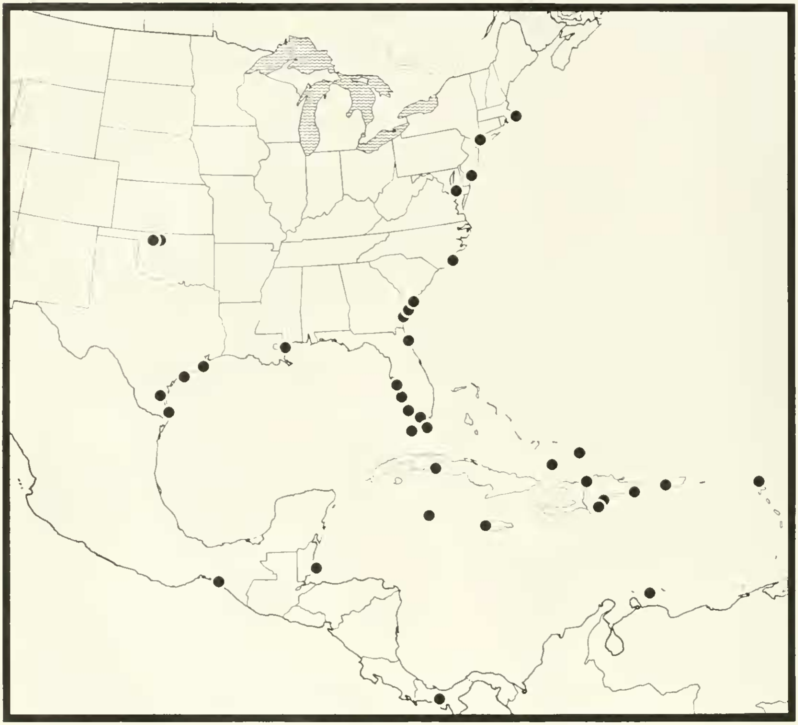


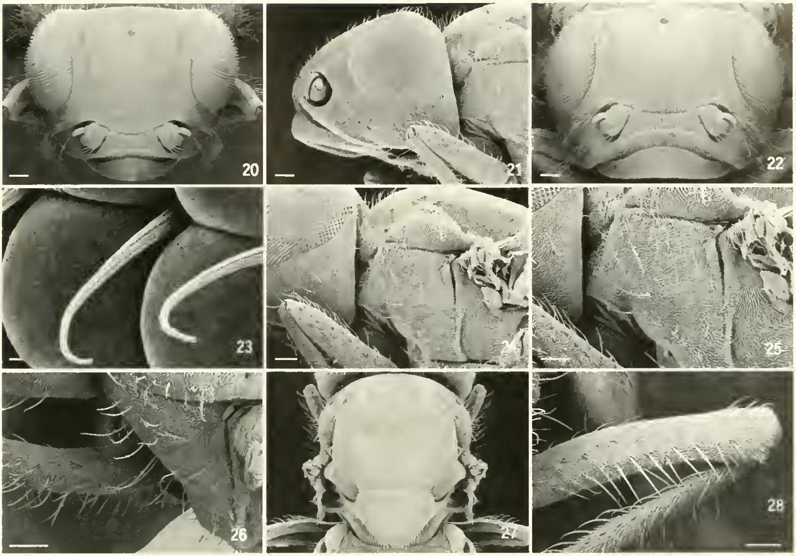
Fig. 19. Distribution map for *Lipochaeta slossonae*.

Thorax (Figs. 24–28): Mesonotum varying from dark brown to dark gray. Anepisternal setae long, setae appearing brushlike; katepisternal seta reduced but other setulae usually evident. Legs, particularly tibiae, bearing long setae, appearing brushlike; apical tarsomere partially to completely darkened.

Abdomen (Figs. 29–30): Surstylus shorter (subequal to height of epandrium), parallel sided to bluntly rounded apex.

Type material.—The holotype ♂ is labeled "CoronaDelMar 29/6/42 [29 Jun 1942] CAL[IFORNIA] AlMelander/AlMelander Collection 1961 [right ⅓ with green stippling]/HOLOTYPE ♂ Lipochaeta ranica W. N. Mathis & Trautwein USNM [red; species name, gender symbol, and "& Trautwein" handwritten]." The holotype is double mounted (minuten in a rectangular card), is in excellent condition, and is deposited in the USNM. Eighty-one paratypes (37 ♂, 44 ♀; USNM) bear the same locality data as the holotype.

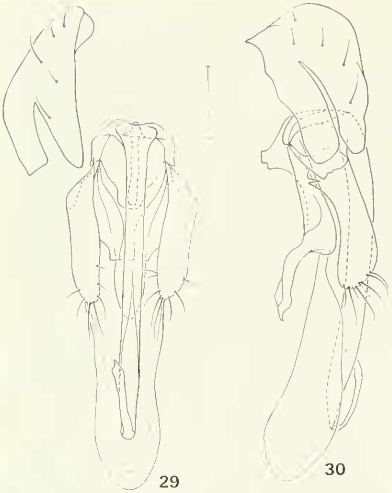
Other specimens examined.—ECUADOR. *Galápagos Islands: Isabela:* Puerto Villamil (littoral, sweeping sand beach), 7 Mar 1989, B. J. Sinclair (5 ♂, 1 ♀; CNC). *Santa Cruz:* Charles Darwin Research Station (littoral, intertidal rocks, beach at high tide line), 17–27 Jan 1989, B. J. Sinclair (10 ♂, 11 ♀; CNC, USNM).



Figs. 20–28. Scanning electron micrographs of *Lipochaeta ranica*. 20, Head, anterodorsal view. 21, Same, lateral view. 22, Same, anterior view. 23, Interfacetal setae, lateroblique view. 24, Left pleural area, lateral view. 25, Left anepisternum, lateral view. 26, Notopleuron and anepisternum, dorsoblique view. 27, Thorax, dorsal view. 28, Left midfemur, anterior view. Scale bar equals 100 μm.

MEXICO. *Baja California Norte:* San Felipe, 19 Feb 1954, P. H. Arnaud, Jr. (15 ♂, 7 ♀; USNM); San Felipe (3 mi N), 25 Mar 1964, M. E. Irwin (2 ♂, 2 ♀; USNM); Ensenada, 24 Jun 1950, A. L. Melander (20 ♂, 16 ♀; USNM); San Quintin, 7 May–25 Sept 1925, 1950, H. H. Keifer, R. L. Langston (3 ♂; USNM); Bellandra Bay: Isla Carmen, Gulf of California, 28 Mar 1953, P. H. Arnaud, Jr. (6 ♂, 6 ♀; USNM); Loreto (Baja), 29 Mar–19 May 1921, 1953, P. H. Arnaud, Jr., E. P. Van Duzee (2 ♂, 12 ♀; USNM). *Nayarit:* Agua Verde Bay, 23 Mar 1953, P. H. Arnaud, Jr. (6 ♂, 1 ♀; USNM); San Blas, 2 Apr 1964, E. I. Schlinger (1 ♂; USNM). *Sonora:* Puerto Peñasco, 28 Apr 1948 (1 ♀; USNM).

UNITED STATES. *California. Los Angeles:* Huntington Beach, 7 Oct 1929, L. D. Anderson (1 ♂; USNM); Laguna Beach, 27 Aug 1943, F. R. Cole, A. L. Melander (2 ♂; USNM); Long Beach, 4 Aug–21 Oct 1911, 1935, R. W. Doane, A. L. Melander (17 ♂, 17 ♀; USNM); San Pedro, 8 Jul 1950, T. D. A. Cockerell (2 ♂; ANSP, USNM); Seal Beach, 26 Jul 1942, A. L. Melander (1 ♂; USNM). *Santa Barbara:* Carpinteria, 12–17 Jun 1955, A. L. Melander (6 ♂, 1 ♀; USNM); Santa Barbara, 6 Jul 1917, J. M. Aldrich (1 ♂, 2 ♀; USNM). *San Benito:* Castroville, 19 May 1950, A. H. Sturtevant (11 ♂, 8 ♀; USNM). *San Diego:* La Jolla, 22 Jun–16 Aug 1935, 1950, M. T. James, A. L. Melander (2 ♂; ANSP, USNM); San Diego, 5 Apr–3 Aug 1915, 1917, 1932, J. M. Aldrich, M. Van Duzee (11 ♂, 12 ♀; ANSP, USNM). *San Francisco:* San Francisco Bay (salt marshes), 11 Oct 1906, R. W. Doane (3 ♂, 1 ♀; ANSP). *San Luis Obispo:* Morro Bay, 30 Aug 1945,



Figs. 29–30. Structures of the male terminalia of *Lipochaeta ranica* (ejaculatory apodeme not illustrated; Mexico. Baja California Norte: San Fellipe). 29, Cerci (left side only), epandrium (left side only), surstylus, aedeagus, aedeagal apodeme, and hypandrium, lateral view. 30, Same, posterior view. Scale bar equals 0.2 mm.

A. L. Melander (1 ♂, 1 ♀; USNM). *San Mateo:* San Mateo, 19 May 1950, A. H. Sturtevant (7 ♂, 2 ♀; USNM).

Distribution (Fig. 31).—Nearctic: USA (CA). Neotropical: Ecuador (Galápagos Islands), Mexico (BCN).

Etymology.—The species epithet, *ranica,* is of Latin derivation and refers to the froglike face of this species. Townsend (1898: 169), in referring to the head of *Lipochaeta,* described it as "frog-mouthed" or "frog-faced," and we concur (Fig. 22).

Remarks.—All specimens from California and Baja California Norte (Mexico) that we have examined were previously misidentified as *L. slossonae* and represent this new species (see species synonymy).

Cheng and Lewin (1974) reported on the peculiar "fluidisation" of the substrate as part of the feeding behavior of this species (as *L. slossonae*). From observations in both the field and laboratory, they discovered that this species fluidizes the wet sand on the beach through a shaking motion that apparently loosens the interstitial microflora, which is then imbibed as a kind of soup.

Variation is evident between some populations of this species. Externally, the specimens from the Galápagos Islands are very similar to *L. slossonae,* especially in the length and number of setae and setulae and to a lesser degree in coloration. Structures of the male terminalia indicate that these specimens are *L. ranica,* however.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance and cooperation of many organizations and individuals who contributed to the field work and production of this paper. To David A. Grimaldi (AMNH), Jon K. Gelhaus and Donald F. Azuma (ANSP), Nigel Wyatt (BMNH), J. Richard Vockeroth (CNC), and their institutions, who loaned specimens, we express our sincere thanks.

The illustrations were carefully inked by Young T. Sohn. Hollis B. Williams provided technical support. Susann Braden and Scott Whittaker assisted with the preparation of the scanning electron micrographs. For reviewing a draft of this paper, we thank Amnon Freidberg, Stephen D. Gaimari, and Tadeusz Zatwarnicki. We are also grateful to David Challinor, former Assistant Secretary for Research, and to Anna K. Bernensmeyer and David L. Pawson, former Associate Directors for Science, National Museum of Natural History, Smithsonian Institution, for financial support to conduct research at The Natural History Museum (BMNH), London, England, through grants from the Research Opportunity Fund. In 1995, 1996, and 1998, field work on the West Indies was funded in large measure by grants from the Biodiversity Program (Biotic Surveys and Inventories, BSI), National Museum of Natural History, Smithsonian Institution (Lynne R.

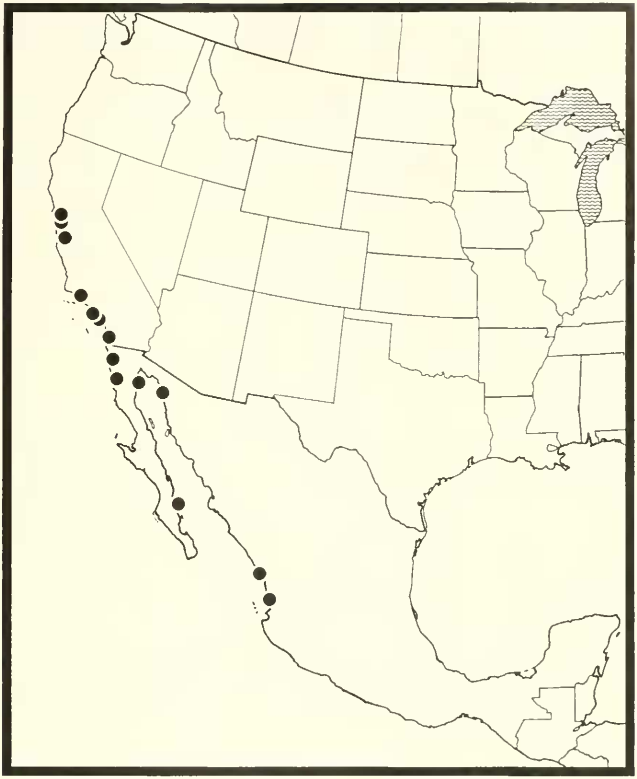


Fig. 31. Distribution map for *Lipochaeta ranica.*

Parenti, former chair, George R. Zug, chair). Field work on the West Indies was greatly expedited through the able and pleasant assistance of N. Dianne Mathis, Hollis B. Williams, Kelvin Guerrero, Daniel E. Pérez-Gelabert, and Oliver S. Flint, Jr. Field work in Guyana was supported by the Smithsonian Institution's Biological Diversity of the Guianas Program (publication number 65; Vicki A. Funk, Director; Carol L. Kelloff, Coordinator).

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